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THE MECHANISM OF EVOLUTION IN THE LIGHT OF HEREDITY AND DEVELOPMENT[1]

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THE general theory of organic evolution undertakes to explain by natural processes the origin of the existing world of living things, and in particular it seeks to account for three classes of phenomena, namely, (1) The diversities (varieties, species, genera, etc.) of the living world; (2) progressive organization (increasing complexity of structure and function) from the lowest to the highest organisms and (3) the fitnesses (adaptations, etc.) of living beings. Its aim is nothing less than a mechanistic explanation of the origin, development and present state of the entire world of life; this is really an enormous undertaking and it is not surprising that this ultimate objective has not yet been reached, indeed it is probable that it may never be fully attained; but at least the problems of organic evolution are in process of being more clearly defined and some promising beginnings have been made toward their solution. To insist, as some have done, that the theory of evolution has failed because it has not yet solved all of these problems is to underestimate both the magnitude of the problems concerned and the progress which has been made toward their solution; to reject evolution, as others have done, because the problems are too great to be solved by the scientific method, is to renounce the slow and sure progress of science in favor of pure speculation and mysticism in which no progress at all is possible.

Scientists no longer discuss the question as to whether evolution has occurred, but there is much conflict of opinion as to how it has occurred. The fact of evolution stands fast; present uncertainties, hypotheses and theories concern only the factors. Unfortunately this distinction between fact and factors has not been appreciated by many persons who are not students of this subject and consequently they have assumed erroneously that doubts as to the latter implied uncertainty as to the former. The two great systems of evolutionary philosophy, known as Lamarckism and Darwinism, are hypotheses as to the factors of evolution, and, if one or both of these should prove to be erroneous, it would not shake our confidence in the truth of evolution itself.

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[1] William Ellery Hale Lectures before the National Academy of Sciences, Washington, April 16 and 18, 1917.

The mechanism of organic evolution is an enormous subject and many phases of it I should be unable to present except in a superficial manner; fortunately a comprehensive discussion of this topic is rendered unnecessary by the lectures of my immediate predecessor in this series.[2] I shall therefore limit my discussion to experimental and analytical studies of inheritance and development in their bearings on evolution. Even in this more limited area I must draw largely upon the work of others. My own researches have lain very largely in the domain of cellular biology and doubtless to many naturalists of the old school this field seems very remote from that of the origin of species. But in biology all roads lead to evolution and, though some of these are highways and others only by-paths, the inhabitant of any quarter of this world may come to its center by the road which passes his own door—by which simile I hope to forestall the criticism that my own field of work does not lie on certain main highways of evolution and that I do not attempt in these lectures to traverse all the routes that lead to the Eternal Theory.

I. EVOLUTION, HISTORICAL AND EXPERIMENTAL

In the development of science there has been a general movement from the methods of observation and description to those of analysis and experiment. Biology as a whole is just now making this transition; physiology has long been experimental, but only within the past quarter century have experimental methods been used extensively in the study of morphology, embryology, heredity and evolution. Biology is no longer a study of living things with the life left out, and evolution is no longer merely a study of the beaches where the tides of life have been. For long, evolution was studied and regarded merely as a past process which had flourished mightily

> In the dark backward and abysm of time

but which had practically ceased to-day. As a historicoscientific subject its results were studied and their cause surmised—all at very long range. As a past process it was approached only through the static branches of biology, such as Classification, Morphology, and Paleontology.

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[2] Henry Fairfield Osborn, "The Origin and Evolution of Life."

1. *Classification and Evolution*

To Darwin and his contemporaries evolution was largely a question of species and their origin, although it is true that Darwin laid much broader foundations for his theory than can be found in Classification alone, extending them into almost every field of biology and thus anticipating many recent developments of this subject. Nevertheless, to most naturalists of that period the transmutation of species seemed to be a problem for the systematists. It was in his famous "Essay on Classification" that Louis Agassiz attacked the new theory, and it was in the field of systematic botany that Asa Gray gave it such effective support. I remember with what scorn I once heard Cope say of Weismann, "He does not know species, and yet he presumes to discuss their origin." Now we ask, "Does any one know species?" and we look to the experimentalist for an answer, for the geneticist has shown how extraordinarily complex a species may be. Now we recognize that the evolution of a Linnean species is a problem akin to the origin of genera or larger groups, to be approached only by analogy and speculation. The experimental evolutionist deals with variations, mutations, elementary or incipient species which can be studied effectively only in pedigreed cultures.

2. *Morphology and Evolution*

The earlier morphologists studied the structure of various organs and systems in different species and in different stages of individual development and guessed more or less shrewdly as to the manner in which these structures had evolved. It is amusing now to recall how almost any group of organisms could be shown, by those who had made a special study of that group, to be ancestral to many other groups and how easy it was to construct "phylogenetic trees" or to explain the origin of particular structures by pure speculation. Whenever modifications of a structure could be arranged in a nicely graded series it was assumed that the actual course of the evolution of this structure had been determined, and not infrequently it seems to have been assumed that the course of evolution revealed its cause. Now we know that the minor changes in evolution do not always occur in a nicely graded series, but sometimes by sudden or discontinuous changes, while the course of evolution reveals only the direction and area in which its causes must operate, but not the causes themselves.

3. *Paleontology and Evolution*

Of all students of evolution the paleontologist has the most direct evidence as to its general course in the past but he has also the most indirect and uncertain means of determining its intimate causes, for he is farthest removed from it as a living process which can be dealt with experimentally. Consequently for the paleontologist as well as for the systematist and morphologist the methods and causes of evolution afforded a fertile field for an active imagination and as a result almost every possible theory was proposed, but none were demonstrated. The subject appealed to imagination, but not to verification.

4. *Experimental Evolution*

As long as evolution was regarded merely as a past process it could be studied only as an historic phenomenon. The recognition of evolution as a present process makes it at once an experimental as well as an historical science, and its problems are not merely those of the systematist, morphologist and paleontologist, but also those of the geneticist, embryologist, cytologist, physiologist, and bio-chemist. In short all branches of biology now center in this great theory. Furthermore, the only possible method of really determining the causes of evolution and of demonstrating the mechanism involved is by means of experiments.

(*a*) *Deals only with Diversities or Minor Changes.*—The study of contemporary evolution must of necessity deal with relatively minute changes in organism, with the production of mere diversities. The greater steps in evolution, such as the origin of species, genera and larger groups, and all progressive evolution, can not be dealt with experimentally unless such experiments are continued for long periods of time or unless artificial means are found of speeding up the evolutionary processes. Indeed it may be objected that until these minor changes have accumulated so that they actually give rise to new species comparable to those existing to-day in nature, we shall not be sure that they are real steps in evolution,—the materials out of which the many diverse forms of animals and plants have come into existence. Unfortunately this is only too true, and consequently evolution in its larger aspects is now and must long remain a theory rather than a demonstration, and yet the evidences that some of these minor changes, such as variations and mutations, are first steps in the making of species and still higher groups is so extremely probable that it would be unreasonable to deny it. It is at least a probable and reasonable hypothesis and we know of no other which is either reasonable or probable.

(*b*) *Rise of Experimental Biology.*—During the last two decades of the nineteenth century the experimental method began to be used in the study of ontogeny and phylogeny and an indirect though most important result of such experiments was the introduction of a more critical spirit into morphology and a growing dissatisfaction with speculations on the course or cause of phylogeny. For some years there was conflict between the "pure morphologists" and the "experimentalists" as to the relative value of observation and experiment, but now so completely has our point of view changed that morphology as a purely observational study of dead "material" has almost ceased to exist, and in many institutions professorships in morphology have become professorships in experimental zoology or botany. And yet there is no magical power in experimental methods which renders the older methods of observation antiquated or useless. As a method of investigation experiment alone is no better and probably is not as good as observation alone; it is only when experimental methods are used to supplement observational ones that the best results are obtained.

(*c*) *Iconoclasm of Experimentalists.*—The experimental method, whether in morphology, embryology, or evolution is "nothing if not critical." In the first enthusiasm for the new method its advocates began by discrediting or discarding conclusions based upon mere observation and reflection. But scientific theories are not necessarily false because they have been come at by observation or logic; clear thinking is essential to scientific progress as well as careful experiments, and brains as well as eyes and hands play an important part in the discovery of truth. Nevertheless there is probably no other scientific doctrine which shows a greater need of caution, criticism and experimental confirmation than does the theory of evolution. In evolution no less than in other scientific fields frequently the most complex hypotheses are devised to account for things which have no real existence, as for example attempts to explain the hereditary transmission of acquired somatic characters, the telescoping of phylogeny into ontogeny, the transformation of one adult organism into another, etc. Science sometimes becomes so lumbered up and confused by many false theories that the best way of advancing knowledge is by clearing the ground of errors, and this is especially true of evolutionary theories because of their appeal to imagination and their difficulty of verification.

(*d*) *Extravagant Hopes of Experimentalists.*—In the first enthusiasm over the application of experiment to the problems of evolution many extravagant hopes and predictions were made. Not only species, but even whole faunas and floras were to be artificially made "while you wait." But organisms have shown themselves to be wonderfully stable and resistant to change. Modifications of all sorts can be produced but few if any of these are inherited. The living thing which is delicate and plastic beyond all comparison is yet remarkably stable and stubborn. The results of experimental evolution as compared with the anticipations of twenty years ago have been distinctly disappointing; and yet progress has been made, and in particular many facts are more definite, many ideas more clear and many old theories have been shown to be untenable while a few have been more firmly established than ever before. Probably more progress has been made since the year 1900 in understanding the factors of evolution than in all previous centuries. And this is true largely because of the epoch-making work which has been done during the past fifteen years in bringing to light the factors of individual development.

5. *Genetics and Cytology—the Recent Lines of Progress*

The two fields in which our knowledge of the causes of evolution has made the greatest and most substantial progress within recent years are genetics and cytology, the one dealing with the inherited characteristics of successive generations of individuals, the other with the cellular bases of these characteristics in the germ cells and the transformations which these undergo in development; the former with the analysis of the developed organism into its constituent characters, the latter with the analysis of the germ cells with especial reference to the material basis of heredity. Although at first these two lines of work seemed very distinct the researches of the past fifteen or twenty years have shown that they are most intimately related and each has shed a flood of light upon the other. In the combination of these two lines of research so totally different in methods and apparently so unrelated in results, our knowledge of the methods and causes of evolution has been greatly extended. For the first time we know pretty definitely where to look for evolutionary changes, for the first time we are getting at the real mechanism of evolution.

Since the rediscovery in 1900 of the long-forgotten principles of inheritance, which were first made known by Mendel in 1866, remarkable progress has been made in the field of genetics—indeed almost all that is known concerning the exact manner of hereditary transmission has been learned since that year, and it is probable, as Morgan has said, that the fundamental principles of such transmission have already been discovered. The great and almost endless problems which stretch out before the geneticist have to do with a more minute study of the factors or causes of hereditary transmission. In similar manner the grosser facts as to the structure and development of the germ cells and as to the transformation of the fertilized egg into the embryo and adult are well known, but we have made the merest beginning in the study of the causes of this development and of the exact manner in which the germinal organization is transformed into developed characters. Development is indeed a vastly greater and more complicated problem than heredity, if by the latter is meant merely the transmission of germinal units from one generation to the next.

Thus the study of genetics, cytology or of any other science repeats the same general process which has characterized the study of evolution itself,—the outstanding facts are first established with relative ease, the factors are determined only after prolonged research. Furthermore the discovery of "the cause" of any phenomenon evermore leads to new inquiries as to the cause of this cause, so that research is never finished and knowledge is never complete.

II. ONTOGENY AND PHYLOGENY

Intimate Relations of the Two

Ontogeny or the origin of individuals and phylogeny or the origin of races are two different aspects of one and the same thing, namely organic development. There is a remarkable parallelism between the two, and in particular the factors or causes of development are essentially the same in both. Phylogeny is a present process as certainly as is ontogeny. Just as the earth rotates on its axis, revolves in its orbit and the whole solar system moves through space, so organisms undergo embryonic development, specific development and phyletic development, all being parts of one great process. All detailed study of evolution is necessarily a study of successive generations of individuals, and all analytical or experimental study of the causes of evolution resolves itself into a study of the factors involved in the genesis of individuals; there is no other possible method of approaching the problem. For this reason the student of ontogeny is especially well fitted to deal with the factors of phylogeny. The study of the factors involved in the genesis of individuals under various conditions of inheritance and environment reveals all that can certainly be known regarding the methods and causes of the evolution of races and species.

1. *Development is Real and not Illusory*

Ontogeny or the development of an individual from the egg to the adult condition consists in progressive, coordinate differentiation of both structures and functions. To a certain extent differentiations are already present in the germ cells, but during the course of development their number is greatly increased. This increase in differentiation is caused by modification of previously existing differentiations, by transformation rather than by formation *de novo,* by evolution rather than by creation. New things appear in the course of ontogeny because of new combinations of things already present, just as new chemical substances with new qualities appear as a result of new combinations of elements.

In similar manner evolution is progressive diversification and adaptation. New species, new adaptations, new forms and new functions appear in the course of evolution because of new combinations of characters already present, or rather of the elements out of which characters are built. If any Mendelian of the stricter sort is inclined to question this statement and to affirm that characters or their germinal factors come out of any combination exactly as they went into it and that they have therefore suffered no permanent change, let him consider that any permanent change or mutation of a germinal factor or gene must consist in some new combination of the elements which go to make up the factor itself. For the very possibility of any change or mutation proves that the thing which changes is composed of more elementary units, and this is true not only of organisms, characters and germinal factors, but also of molecules and atoms. Those things only can be absolutely changeless which are absolutely elemental, and *vice versa,* those only are absolutely elemental which are absolutely changeless. *Organic evolution must of necessity consist in new combinations of the parts of which organisms are composed, whether those parts be organs, characters, genes, molecules or atoms.*

Neither ontogney nor phylogeny consists in making visible what was present but invisible before, much less is it a mere simplification of an original complex by a sorting out of certain characters or factors of characters. It will be shown in a later section that ontogeny does consist to a certain extent in sorting out different materials present in the egg and in the isolation of these materials in different cells, but there is also a progressive formation of new materials during the course of development; there is in development real increase of complexity in which new characters appear by a process of "creative synthesis"; new combinations of the same old elements give rise to new qualities, new forms, new functions. In short, development is real and not illusory, and what is true of ontogeny in this respect is equally true of phylogeny.

2. *Development is Progressive and not Retrogressive*

Of all false theories and erroneous opinions one of the most far-reaching and misleading in its effects is that which may be called the inverted view of development, a view which regards the adult organism as the starting point in ontogeny or phylogeny and which then attempts to explain the transfer of developed characters from this to the germ. This inverted view of development is responsible for almost all of the false theories of development and evolution which now incumber the science of biology.

(*a*) *Inverted View of Ontogeny.*—Before Weismann a false trend was given to theories of development by neglecting or misconstruing one of the most elementary facts of ontogeny, viz., that development proceeds from the egg to the mature organism and not in the reverse direction. It was known, of course, that the egg produces the hen, but it was believed that the hen in turn produces other eggs, so that the life cycle was thought to consist of a progressive phase from egg to hen and a regressive phase from hen to egg (Figs. 1 and 2). It seemed evident that the mature organism manufactured the germ cells, and consequently, it was supposed that characters of the adult organism could be "reflected on" or condensed in the germ cells and then reappear in the next generation. Darwin's hypothesis of "pangenesis" made this general conception more precise by assuming that every cell of the body contributes particles or gemmules to the formation of the germ cells.

Based on Erroneous Cell Theory.—This inverted view of development, namely that mature organisms make the germ cells, is the result in large part of erroneous opinions as to the manner of origin of cells in general and of germ cells in particular. From the time of the work of Casper Friedrich Wolff (1759) to that of Remak (1841) it was maintained that "ves-

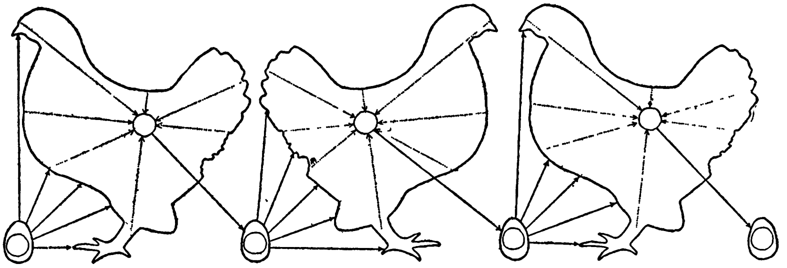

FIG. 1. DIAGRAM SHOWING THE ERRONEOUS VIEW THAT THE BODY OF HEN PRODUCES THE EGG (dotted arrows), while the latter in turn produces the body of the hen but not the egg.

icles" or cells appeared as droplets in a fundamental substance, or "as bubbles of gas appear in fermenting dough." New cells were supposed to appear between the old ones by a process known as "free cell formation." A principal feature of the cell theory of Schwann (1839–41) was that new cells arise in a homogeneous ground substance, the cytoblasteme, "like crystals in a mother liquor." On the other hand Remak (1841) proved that cells arise by division of preexisting cells, but for a long time "free cell formation," or the formation of cells *de novo*, was still maintained to be one of the methods by which new cells arise.

This antiquated conception as to the origin of cells is still responsible for much rubbish in our theories of evolution and development, for even at the present day many theories which grew up under this old conception are still maintained. If earlier evolutionists had known that every cell comes from a preceding cell by division and that it thereafter remains absolutely distinct from other cells, taking into itself no living substance from without but manufacturing its own protoplasm from food substances, there probably would have been no doctrine of "pangenesis," of the "reflection of adult characters on the egg," of the inheritance of developed somatic characters—no inverted views of development, heredity and evolution.

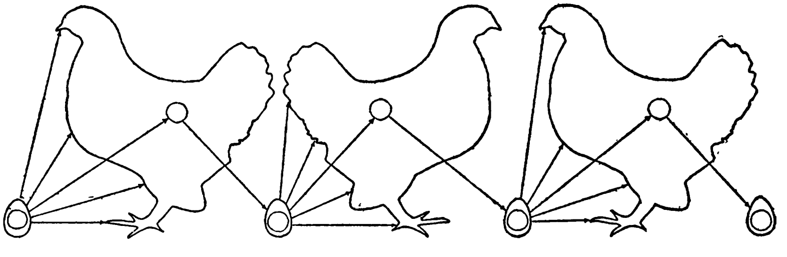

FIG. 2. DIAGRAM SHOWING THE TRUE VIEW THAT THE EGG PRODUCES THE BODY OF THE HEN AND ALSO THE EGG.

The cellular history of development has demonstrated that adult organisms do not manufacture germ cells and transmit their characters to them. Neither germ cells nor any other kind of cells are formed by the body as a whole, but every cell in the body comes from a preceding cell by a process of division and it grows, not by contributions of protoplasm from other cells, but by building up its own protoplasm from food substances; and germ cells are formed not by contributions from all parts of the body, but by division of preceding cells, which are derived ultimately from the fertilized egg. Development is not a process which goes forward at one phase and backward at another, but is always and everywhere a progressive movement from the egg to the adult and never one in the reverse direction (Fig. 3). End stages are not added on to previously completed ontogenies for every inherited change, whether of an end stage or of an earlier one must be represented by some change in the germ cell itself.

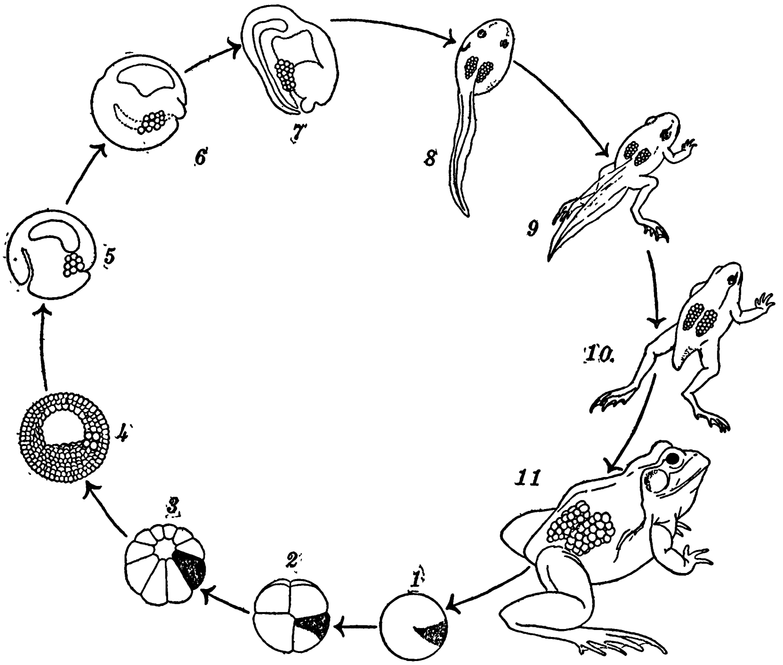

FIG. 3. DIAGRAM OF LIFE CYCLE OF THE FROG SHOWING THE STEPS BY WHICH THE EGG GIVES RISE TO THE BODY OF THE FROG AND TO OTHER EGGS. 1. Fertilized egg; the stippled area is the mesodermal crescent from which the germ cells come. 2. Eight cell stage. 3. Thirty-two cell stage. 4. Blastula showing germ cells in heavy outline. 5–7. Early to late gastrulæ showing germ cells in heavy outlines. 8–9. Early and late tadpoles with germ cells as in preceding figures. 10–11. Metamorphosing and adult frogs containing germ cells which come in direct lineage from the egg shown in 1.

(*b*) *The "Recapitulation Theory."*—That there is a certain parallelism between the stages of ontogeny and those of phylogeny has long been known, but there has been much difference of opinion, and there is now a widespread misunderstanding as to the significance of this parallelism.

(1) *Truth and Error of Theory.*—The "fundamental biogenetic law" of Haeckel affirms that "ontogeny is a brief recapitulation of phylogeny" or, as some one has picturesquely expressed it, "every organism climbs its own ancestral tree."

Various other hypotheses such as Lankester's "precocious segregation" and Hyatt's "law of acceleration" taught that adult characters tend to appear at earlier and earlier stages in ontogeny, because they are "reflected back upon the germ cells" and thus that what were at one time "end stages" in ontogeny are crowded back into earlier stages, while new end stages are added. The "fundamental biogenetic law" of Haeckel was based entirely upon this idea that in the course of evolution new end stages are added to the ontogeny as it had previously existed. This conception may be represented by the following diagram in which the successive stages in phylogeny and ontogeny are represented in alphabetical series:

Phylogenetic Series	Ontogenetic Series
A	A
B	AB
C	ABC
↓ D	ABCD
	→

Thus the ontogeny of each of these phylogenetic stages was supposed to recapitulate the entire evolutionary series.

And yet among higher forms there are very many adaptations to embryonic and larval life which have no counterpart in lower forms and which indeed could not exist in free-living organisms; such are the embryonic membranes of higher vertebrates, the yolk-sac of fishes, and the modifications of development in these forms and in many of the invertebrates due to the presence of much yolk, the extraordinary modification of the larvæ of many parasites, and the remarkable differences in development which are found in different species of almost every class of animals. Such differences in the ontogenesis of organisms which are otherwise closely alike demonstrate that certain evolutionary changes may occur in embryonic stages without greatly modifying adult stages.

On the other hand, in many cases adult stages have undergone much greater changes than have embryonic ones; for example Ascidians are known to belong to the phylum Chordata, *Sacculina* to the Arthropoda, *Myzostomum* to the Annelida, etc., only because in these cases embryonic or larval stages preserve ancestral characters long after adult stages have lost them. In short *evolutionary changes may affect any portion of the life history, and therefore the course of ontogeny is not a sure indication of the course of phylogeny.*

It thus became evident that earlier phylogenetic stages were not always reproduced in the ontogeny and consequently a distinction was made between those ontogenetic stages which repeated the phylogeny and were called by Haeckel "palingenetic" and those which did not and were called "cœnogenetic." Consequently the phylogenetic and ontogenetic series were represented as follows:

Phylogenetic Series	Ontogenetic Series
A	A
B	aB
C	abC
↓ D	abcD
	⟶

Or since ontogeny is greatly shortened as compared with phylogeny the course of the two might be represented by the diagram on p. 494 (Fig. 4).

(2) *Embryonic Homologies and their Causes.*—Nevertheless, many organisms which differ widely in adult stages reveal a surprising degree of resemblance in embryonic stages and in general embryonic resemblances appear to be more persistent than adult ones. It is certainly no mere accident that practically all animals begin their individual existence as fertilized eggs, that before or during fertilization all eggs produce two polar bodies, that in animals as far apart as flatworms, annelids and mollusks the early cleavages of the egg are fundamentally alike and that where differences exist they have led to the discovery of rudimentary cells in one form corresponding to well-developed cells in another (Fig. 5). It is no accident that the eggs of all chordates have the same type of cytoplasmic localization, that all develop a notochord and nervous system and mesoderm in fundamentally the same way, that all vertebrates whatever have gill slits in embryonic or adult stages, etc. These and thousands of other resemblances of the same sort can be explained only by assuming that they are homologies or inherited likenesses and that forms showing these likenesses are genetically related. But this does not mean that in higher animals addi-

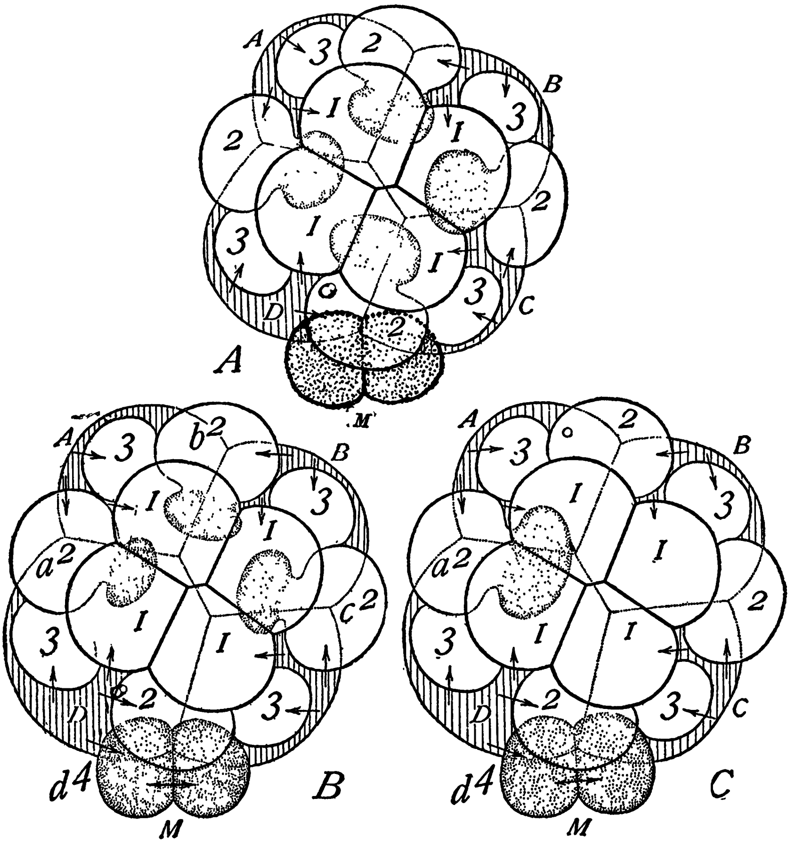

FIG. 4. ANCESTRAL REMINISCENCE IN CLEAVAGE. Showing homologous cells in *A*, a polyclade (*Leproplana*) ; *B*, a gasteropod (*Crepidula*) ; *C*, a lamellibranch (*Unio*). (Modified from Wilson.)

tional stages have been added on to those present in lower forms or that adult stages of lower animals have been crowded back into the embryonic life of higher forms as the recapitulation theory assumed. It does not mean that all organisms are alike in early stages of development and that they first become unlike in later stages. We now have direct evidence that several distinct types of animals have distinct types of eggs; thus there are the (1) Cœlenterate, (2) Polyclade-Annelid-Mollusk, (3) Echinoderm, (4) Nematode and (5) Chordate types of egg organization and these do not converge to a common type in the earliest stages of ontogeny (Fig. 6). Echinoderms come from echinoderm eggs, mollusks from mollusk eggs, vertebrates from vertebrate eggs and " the egg of a frog is as different from the egg of a hen as a frog is from a hen."

There are differences of a fundamental order, even in the earliest stages of development, between a vertebrate and an invertebrate, and the early development does not reveal the

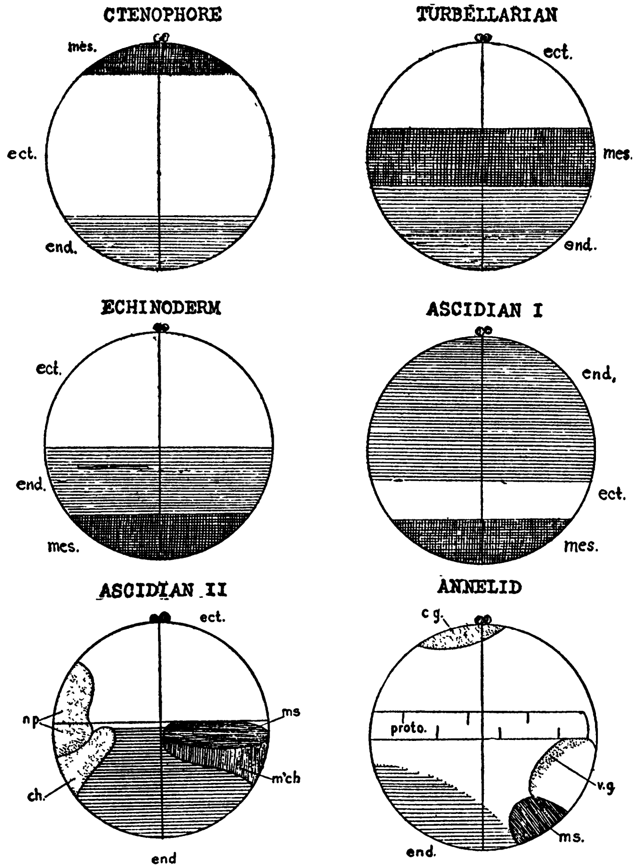

FIG. 5. TYPES OF EGG ORGANIZATION IN DIFFERENT ANIMAL PHYLA. Cross hatched area mesoderm or mesenchyme (*mes*); horizontal lines endoderm (*end*); unshaded area ectoderm (*Ect*). In the first four figures the pattern of localization is that found about the time of the first cleavage; in the last two figures the pattern is that found at a later stage; *n.p.*, neural plate; *ch.*, chorda; *c.g.*, cerebral ganglion; *v.g.*, ventral ganglion; *proto.*, prototroch.

manner in which the one may have been derived from the other. The annelids do not approach the chordates or echinoderms in the earliest stages of development any more closely than in the later stages (Fig. 6). In short there is no convergence toward a common type as one goes back to earlier and earlier stages of

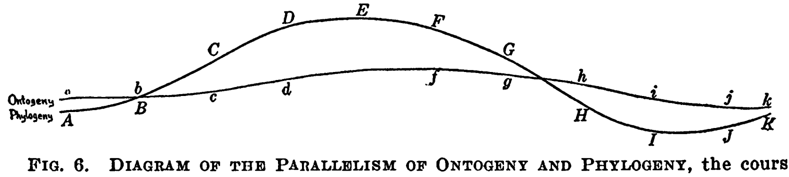

FIG. 6. DIAGRAM OF THE PARALLELISM OF ONTOGENY AND PHYLOGENY, the course of the latter being more roundabout and of the former more direct. Where ontogeny follows phylogeny most closely we have *palingenetic* stages, where it departs from phylogeny the stages are *cœnogenetic*.

ontogeny. The recapitulation theory assumes that there is such a convergence in the early stages, but on the other hand the accurate study of the "cell lineage" of eggs and embryos shows that the resemblances and differences between different animals in the earliest stages of development are of the same order of magnitude as those between later stages. Homologies of cleavage must be due to similarities in the protoplasmic organization of the cleavage cells, and the same must be said of homologies of eggs before cleavage begins. Similarities in the protoplasmic substances of eggs and in the pattern of localization must lie at the bottom of all later appearing similarities.

The cause of all embryonic homologies is therefore the same as the cause of adult homologies, viz., inherited likeness in the protoplasm due to community of descent, and it is only because there is increase of specialization as development progresses that the most general resemblances are found in the earliest stages, while more special resemblances occur only in later ones. This alone explains the fact that embryonic resemblances are on the whole more persistent than those of the adult.

(3) *Resemblances in Functions and Processes more General than in Structures.*—The stages of phylogeny are not exactly repeated in the ontogeny because all conditions both intrinsic and extrinsic are not the same, but the principles of *heredity* and *variation,* of *differentiation* and *development,* are everywhere the same in all plants and animals and men, and these principles of ontogeny are at the same time the principles of phylogeny. Ontogeny recapitulates phylogeny not in all its stages and forms, but in its *factors* and *principles.* All the fundamental principles of evolution from ameba to man are involved in the development of a single link in this long chain.

(*c*) *Inverted View of Phylogeny.*—A false trend was given also to all theories of evolution before Weismann by failing to give sufficient attention to the fact that the germ cells are the only bond between species as well as between generations. In older theories of evolution the great fact of ontogeny was neglected and it was generally assumed that one mature form underwent modification by which it was transformed into another. Adult stages of different types were compared and it was shown how one could be derived from the other by turning it upside down, by closing up the old mouth and opening a new one somewhere else, and by making other equally radical changes in a fully developed organism (Fig. 7). Ontogeny was temporarily forgotten and the fact was overlooked that mature organisms do not produce mature organisms, but that each generation arises from germ cells which alone are continuous from generation to generation.

Until recently, evolution was regarded almost entirely from the standpoint of the developed organism. The great problem of evolution was supposed to be the method by which one type of developed animal or plant gave rise to another type. Mature organisms are known to undergo changes in response to environment or to conditions of life and these changes were regarded as evolutionary ones. Thus Lamarck supposed that the numerous modifications which adult plants and animals undergo in response to conditions of climate, food, use or disuse, etc., are real evolutionary changes which convert one type into another, and even down to the present time there are many naturalists who hold the same view. Indeed many scientists who would refuse to be classified as Lamarckians, because of some minor disagreement with the views of the great French naturalist as to the cause of evolutionary changes or their method of inheritance, nevertheless hold against all opposition the *main tenet of Lamarckism, viz., that evolutionary changes are first wrought in mature organisms.* The classical illustrations of this, which were cited by Lamarck, are familiar to every one, such as the elongation of the neck and forelegs of the giraffe by attempting to reach higher leaves on trees, and the loss of limbs in snakes because of disuse in the narrow quarters in which they live. Many somewhat similar illustrations of this view that evolutionary changes first appear in adult organisms were cited by Darwin, such as the reduction or loss of wings in certain birds or the loss of eyes in cave animals, owing to disuse. More recent literature is filled with such instances; I need only refer to the opinions of many paleontologists, whose studies must of necessity be confined largely to mature organisms, that evolutionary changes take place in these

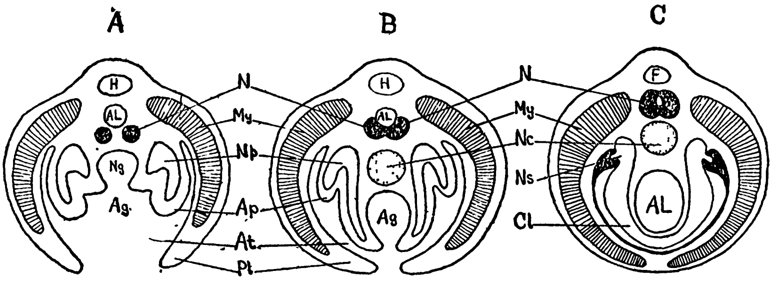

Fig. 7. Diagrams of the Supposed Origin of Vertebrates from Trilobite-like Ancestors, according to Gaskell. Cross sections of the body of (*A*) Trilobite, (*B*) Intermediate form, (*C*) Vertebrate. The alimentary canal (*AL*) of the Trilobite becomes the neural canal (*N*) of the vertebrate, while the alimentary canal of the latter is derived from a groove on the ventral surface of the Trilobite's body (*Ag*) which is folded in to form a tube. The notochord (*Nc*) is likewise derived from a ventral groove (*Ng*) of the Trilobite's body. *H,* heart; *My,* myotome; *Np,* nephrocoel; *Ap,* appendages; *At,* atrial chamber; *Pl,* pleuron; *F,* fat body; *Cl,* coelom.

organisms by the addition of new "end stages" to those previously present; or to the views of the older anatomists that inverse symmetry, or "situs transversus," is caused by the transposition of developed organs from one side of the body to the other; or to the various theories as to the origin of vertebrates from actinians, nemerteans, annelids, arachnids or other invertebrates, by the inversion of the developed bodies of the latter and the transposition and transformation of certain organs (Fig. 7). Indeed all persons are by nature Lamarckians, and for this very reason that attention is focused upon adult organisms which are seen and known of all men rather than upon the germ cells which are usually unseen and unknown.

In all of these cases modifications of adult organisms were supposed to have brought about the changes from one species to another or from one phylum to another. The great problems of evolution were (1) to determine how these adult changes were produced and (2) to show how they were carried over or "transmitted" from one generation to the next. With regard to the last named problem it was evident that these adult changes, if they were to be handed on must be impressed in some way upon the germ cells, since the germ cells form the only living connection between successive generations. Consequently various hypotheses arose, such as were described in the previous section, to show how adult characters might be "reflected" back upon the earlier stages of ontogeny or even upon the germ cells themselves.

(*d*) *Inverted Views of Heredity or the Inheritance of Acquired Characters.*—This is what was originally meant by the phrase "inheritance of acquired characters," namely that changes in adult structures and functions are in some way impressed upon the germ cells so that these identical changes are thereafter inherited. Darwin was the first to suggest a possible mechanism for such inheritance of adult characters in his "Provisional Hypothesis of Pangenesis." He assumed that every portion, perhaps every cell, of the developed organism gave off minute living units or "gemmules" and that these gemmules accumulated in the germ cells and in the course of the development of these cells the gemmules became active and gave rise to parts or cells similar to those from which they originally came. Incredibly complex as such a process must be in normal ontogeny, it became still more complex when the attempt was made to explain the "inheritance of acquired characters," for since *ex hypothese* such characters can be acquired and reappear in offspring at any period in ontogeny it was necessary to assume that these gemmules were given off from all the cells at every period of life. Apart from positive disproof of the hypothesis which was quickly furnished by Galton, it must have broken down from its own weight of incredible assumptions and additional hypotheses.

Since Darwin's time many attempts have been made to devise a more acceptable hypothesis to explain the mechanism of the "inheritance of acquired characters." Many of these are mere modifications of Darwin's hypothesis of pangenesis; others involve the transmission from the body to the germ cells of other, and usually more mysterious, things than gemmules. Among these are supposed "impressions," either nervous, psychic, or mnemonic, but in every instance these speculations follow Darwin's hypothesis in supposing that something proceeds from every part of the adult organism to the germ cells and so modifies those cells that in the course of their development they reproduce the very stages and changes which the adult organism first manifested. They are built on the erroneous idea that the body makes the germ cells; they represent the inverted view of development.

These hypotheses are not only pure assumptions, but in the main they have been invented to explain phenomena which are themselves pure assumptions. Thirty-five years ago Weismann boldly challenged the generally accepted doctrine that "acquired characters" *are* inherited, and from that day to this probably not a single case of such inheritance has been demonstrated, while most of the supposed cases of such inheritance could be better interpreted in some other way. Those who still believe in such inheritance are compelled to admit that it occurs very rarely and exceptionally if at all.

The older ideas of inheritance represented developed characters as being transmitted from one generation to the next; a son was said to have inherited his father's nose or his mother's eyes as if these developed characters were transmitted unchanged. But such a view entirely overlooked the facts of development; characters are never transmitted but only the germinal elements or "factors" of characters and characters develop from these only under the influence of environment, so that every developed character is due to both inheritance and environment. The distinction between inherited and acquired characters is therefore not a logical one, for every developed character is both inherited and acquired. In its original meaning, therefore, the term "inheritance of acquired characters" may be dismissed as not only illogical, but as also impossible in sexual reproduction.

Unfortunately this expression is now used not only in its original sense but also with a very different meaning, viz., the modification of the germplasm through environmental influences, or more briefly the "inheritance of germinal modifications." Indeed the latter is all that is usually meant when the former expression is used, for few if any persons would now maintain that developed characters can enter into or impress themselves upon the germ cells so as to be born again in the next generation. On the other hand it is quite possible that environmental influences may act upon the germ cells so as to alter their hereditary constitution. Whether this possibility is ever realized, whether extrinsic conditions may ever modify the germplasm so as to produce permanent changes in heredity, is the central problem of evolution.

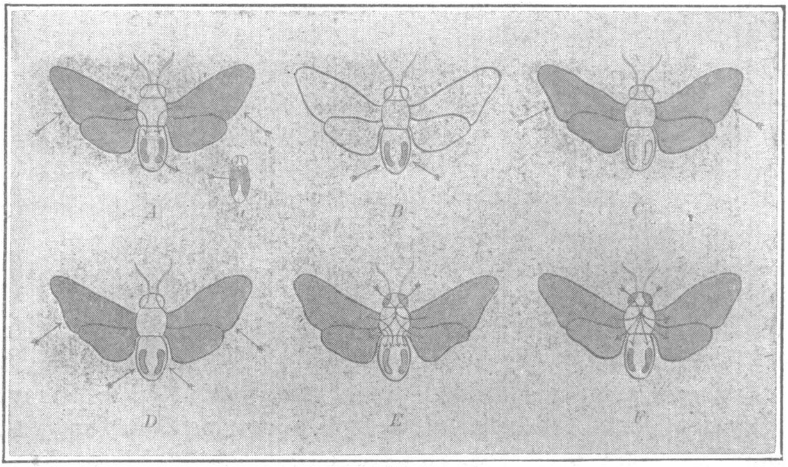

FIG. 8. DIAGRAM TO SHOW THE VARIOUS WAYS IN WHICH ENVIRONMENT MIGHT INFLUENCE THE GERM CELLS. *A*. Environment modifies the body and the latter, the germ cells so as to produce identical modifications in the next generation (*a*); this is "inheritance of acquired characters." *B*. Environment modifies the germ cells but not the body. *C*. Environment modifies the body but not the germ cells. *D*. Environment acts independently upon both body and germ cells. *E*. Environment acts through nervous system on different parts of the body which parts in turn modify the germ cells. *F*. Environment acts through nervous system upon various parts of the body and at the same time upon the germ cells.

It is conceivable that the environment may modify the germ cells in one or more of the methods shown in the accompanying diagram (Fig. 8). In A the environment is supposed to modify the body or soma, which in turn modifies the germ cells so that they produce a body modified like the parental one; this is typical inheritance of an acquired character, and it probably never takes place. In B the environment is shown acting directly upon the germ cells but not upon the body, and in C upon the body but not upon the germ cells, while in D the environment acts independently upon body and germ cells. Probably all of the conditions shown in B, C and D actually exist but it should be noted that when germ cells are modified by environment these modifications are not identical with those of the body nor do they develop into such modified bodies; in short in these three cases there is no inheritance of acquired characters. Finally in E and F are shown two possible ways in which environment may influence the germ cells through the body; in E the environment is supposed to act through the nervous system on various parts of the body, which parts in turn act upon the germ cells; while in F there is parallel action, through the nervous system, upon various parts of the body and also upon the germ cells. There is no satisfactory evidence either for or against the conditions shown in E and F and it is possible that they as well as B, C and D may represent actual conditions. Only against the condition shown in A, that is against the inheritance of acquired characters in the original sense, is the evidence conclusive.

While it is undoubtedly true that the egg produces the hen and other eggs, and that the hen, that is the body or soma, does not *produce* the egg, it is equally true that the body of the hen, which is the environment of the ovarian egg, may *modify* the egg just as the external environment may modify the organism as a whole. But experience shows that such modifications are usually not inherited, they come and go with changing environment, they represent indeed the reactions of a relatively stable organism to an unstable environment. Least of all do these modifications of the germ or of the developed organism *resemble* the changes of the internal or external environment which called them forth; a hen with an artificially modified ovary or oviduct or thyroid gland may possibly produce a modified kind of egg, but there is no more reason for supposing that the chick into which this egg develops will show the same modification of ovary, oviduct or thyroid gland than there is for supposing that a cold climate will produce a race of cold-blooded animals or a vegetable diet a species of vegetable-like animals,—and this because the responses of a germ or of a developed organism to its environment in no way *resemble* that environment. The darkness of caves does not *produce* the blindness of the animals that live in them, much less does it modify their germ cells in such a particular way that they in turn produce blind animals; it is possible, though it has never been proven, that environmental changes may cause changes in the germplasm, but it is extremely improbable that these changes are of such a sort that they will lead, after a long process of development, to the production of just such adult characters as are adapted to the environment which caused the germinal change. Such a view involves on the part of the germplasm such a foreknowledge of future events and contingencies as could not logically be ascribed to deity itself, and which is impossible of scientific formulation or explanation. If environment ever modifies germplasm it is safe to say that these modifications neither *resemble* the environment nor, except in rare circumstances and by chance, are they *adapted* to develop into organisms which will be fitted to that environment.

Probably germ cells may be modified by the soma within which they develop as well as by outside conditions, by internal and also external environment, but there is no justification in this fact for the claim which is often made that "adult characters are reflected" from the soma to the egg or that the environmental modifications of the parents produce identical modifications in offspring,—no evidence for the opinion that because "the parents have eaten sour grapes the children's teeth are set on edge." Further consideration of the effects of external and internal environment on germplasm will be considered in a later section.

In short, development is progressive and not retrogressive, the germ cells are descended from germ cells of the preceding generation and not from the somatic or body cells by which they are surrounded, and while these somatic cells may influence or modify the germ cells by chemical products such as enzymes and hormones and possibly also in other ways, these modifications are usually temporary and are not inherited, and, contrary to the old doctrine of "inheritance of acquired characters," they do not resemble the stimulus which called them forth nor forecast the needs of the future organism into which they will develop. Even when inherited modifications are produced in germs cells by changes in the external or internal environment these modifications may not resemble those produced in somatic cells, and in no instance is there any evidence that modifications of somatic cells are transmitted from these to the germ cells.

The Lamarckian philosophy, under whatever name it appears, is based upon a belief in vitalism or preformation; either the germ foreknows the future needs of the organism by some mysterious vitalistic power, or it is the miniature of the adult and reacts to environment in the same way as the adult does. Neither of these suppositions accords with known facts, and both are contradictory to the spirit of science, for the one makes effects determine causes rather than the reverse, while the other affirms that causes and results are identical. It will always be one of the marvels of the history of science that whole generations of more or less thoughtful men, who were more or less acquainted with the phenomena of organic development could have wandered about so long in such a stupid maze.

(*e*) *The Inverted View of Selection.*—The inverted view of development lurks in many theories where it would least be expected; not merely in the transmutation of one developed species into another, and in the inheritance of acquired characters, but also to a certain extent in selection theories, for in both artificial and natural selection it is usually assumed that evolution takes place by the elimination of developed organisms and that individuals which survive "transmit their characters" to their offspring or "produce germ cells like those from which they came." Of course no adult characters are "transmitted" to offspring and no developed organism "produces" germ cells, but apart from this criticism of the terms used, which may or may not be associated with the inverted view of development, all recent studies of heredity show that not all the different germ cells of an individual are genetically alike except when that individual is absolutely homozygous, a condition which rarely occurs among sexually reproduced organisms, so that the adult organism selected may or may not contain germ cells which are like those from which it came. Thus if the hereditary constitution of the maternal germ cell is represented by *ABC* and that of the paternal cell by *abc*, the offspring would give rise to no less than eight different types of germ cells, only one of which would be like the maternal and one like the paternal cell as is shown in the accompanying diagram:

$$\left.\begin{matrix}\text{ABC}\\ \text{a b c}\end{matrix}\right\} = \begin{matrix}\text{ABC, aBC, AbC, ABc}\\ \text{abc, Abc, aBc, abC}\end{matrix}$$

Pearl has shown that some of the conflicting results as to the influence of selection in evolution may be attributed to this fact. Consequently the selection of developed organisms in the hope of thereby isolating particular germinal types is a blind and imperfect process, though it is the only possible method of procedure, since the hereditary constitution of germ cells can not be recognized directly. Nevertheless it is necessary here also to avoid the inverted view of development involved in the assumption that a certain type of adult organism "produces" germ cells of the same type.

Furthermore the opinion that the principal activity of selection is in the elimination of developed organisms directly reverses the known facts in the case. Elimination is most severe in germ cells and embryonic stages. Where one adult is eliminated tens of embryos and thousands of germ cells are eliminated. These matters will be treated more fully in the section on selection.

(*f*) *The Inverted View of Adaptation.*—Akin to these inverted views of development which put the adult before the germ, the effect before the cause, the end before the beginning, are those views of adaptation which represent needs, advantages and ends as causes of organic fitness. According to these views there is present in organisms a guiding or perfecting principle, an "entelechy," "élan vital" or other unknown cause, which leads to definite and purposive results, just as human intelligence does. It is said by certain philosophical biologists that evolution and adaptation should be looked upon from the standpoint of man, their highest product, rather than from the standpoint of the simplest organisms; evolution should be explained as the result of intelligence and purpose rather than attempt to explain intelligence and purpose as the effects of evolution. In short, according to this view, fitness, purpose and intelligence are causes rather than effects of evolution and adaptation.

But there is no sufficient evidence that even in human intelligence and purpose the usual rule of cause and effect is reversed, and there are many evidences that this is not the case. In human behavior the remembered results of many previous experiences enter as causes into future actions which may thus be directed to desired ends; human intelligence and purpose have thus been built up out of sensations, reactions and remembered experiences. Probably a similar explanation may be given of the adaptive behavior of many organisms, for if results of previous experience may be conserved to any extent in protoplasm then subsequent reactions may be explained as the result of past experience, the elimination of useless reactions and the persistence of useful ones. And in similar manner all kinds of adaptations may be explained as the result of the Darwinian principle of the elimination of the unfit and the survival of the fit. There is therefore no necessity for assuming that needs, advantages and ends serve as causes of adaptation. This inverted view of cause and effect is as unnecessary as is the inverted view of development.

On the other hand certain philosophers and biologists maintain that the responses of organisms to stimuli are always adaptive; Bergson in particular has supported this hypothesis. That there is considerable evidence in favor of such a view may seem to be proven by many well-known instances of regulation and regeneration, by many protective and preservative reactions which one finds in organisms; just as the soma usually responds to stimuli in adaptive ways, so it is maintained the germplasm also responds adaptively. However, Darwin and many others have shown conclusively that somatic responses are not always adaptive and that those which are such vary greatly in degree of perfection. That every change in the germplasm is an adaptive change to the environmental stimulus which called it forth is a thesis impossible to maintain, as is demonstrated by all recent work on mutations. Most of these mutations are positively injurious and do not in any degree make the organism better adapted to the conditions in which they arose. Furthermore it should be noted that the assumption that germplasm may respond adaptively to external stimuli really signifies that the germplasm responds in such a way that the developed organism to which it gives rise is better adapted to the environment and not that the germplasm itself is better adapted; therefore if such beneficial responses really occurred they would be beneficial only in an anticipatory way and they would be beneficial to the germplasm only secondarily and very indirectly. This hypothesis also is based upon the inverted view of development, namely, that developed organisms create and control the germplasm rather than the reverse. The fact is that there is no evidence that either germplasm or somatoplasm always responds to the environment in a directly beneficial way. The usual beneficial character of responses must be explained in some other manner.

In conclusion, all hypotheses which assume that evolutionary changes first occur in developed organisms and are then "impressed" in some manner upon the germ cells neglect entirely the well-known fact that development is not a reversible process; a man can not enter a second time into his mother's womb and be born again and a developed organism can not again become an egg. Consequently all such hypotheses not only put the cart before the horse, but they put the end of the journey before its beginning. It is now plainly apparent to those who have considered the problem of evolution most seriously that evolution must take place by modifications of germ cells or of germplasm rather than of adult organisms. Consequently all the older theories of evolution and many of the newer ones which are based upon that ancient and erroneous idea that the hen produces the egg and not the egg the hen may be dismissed without further consideration here. They represent an untenable and inverted view of organic development, for while it is absolutely certain that the fertilized egg produces the developed organism it is equally certain that the latter does not produce the former, but that every germ cell comes in direct lineage from the germ cells of the preceding generation.

(*To be continued*)